

**Survey of Gelatinous Zooplankton ("Jellyfish")
in the San Francisco Estuary:
Initial Field Survey, Annotated Species Checklist, and
Field Key**

John T. Rees
Bay-Delta Area Shore Institute
California State University, Hayward

and

Christopher L. Kitting
Bay-Delta Area Shore Institute and Department of Biological Sciences
California State University, Hayward

August 2002

**Technical Report 70
Interagency Ecological Program
for the San Francisco Estuary**

A Cooperative Program of the

California Department of Water Resources
State Water Resources Control Board
U.S. Bureau of Reclamation
U.S. Army Corps of Engineers

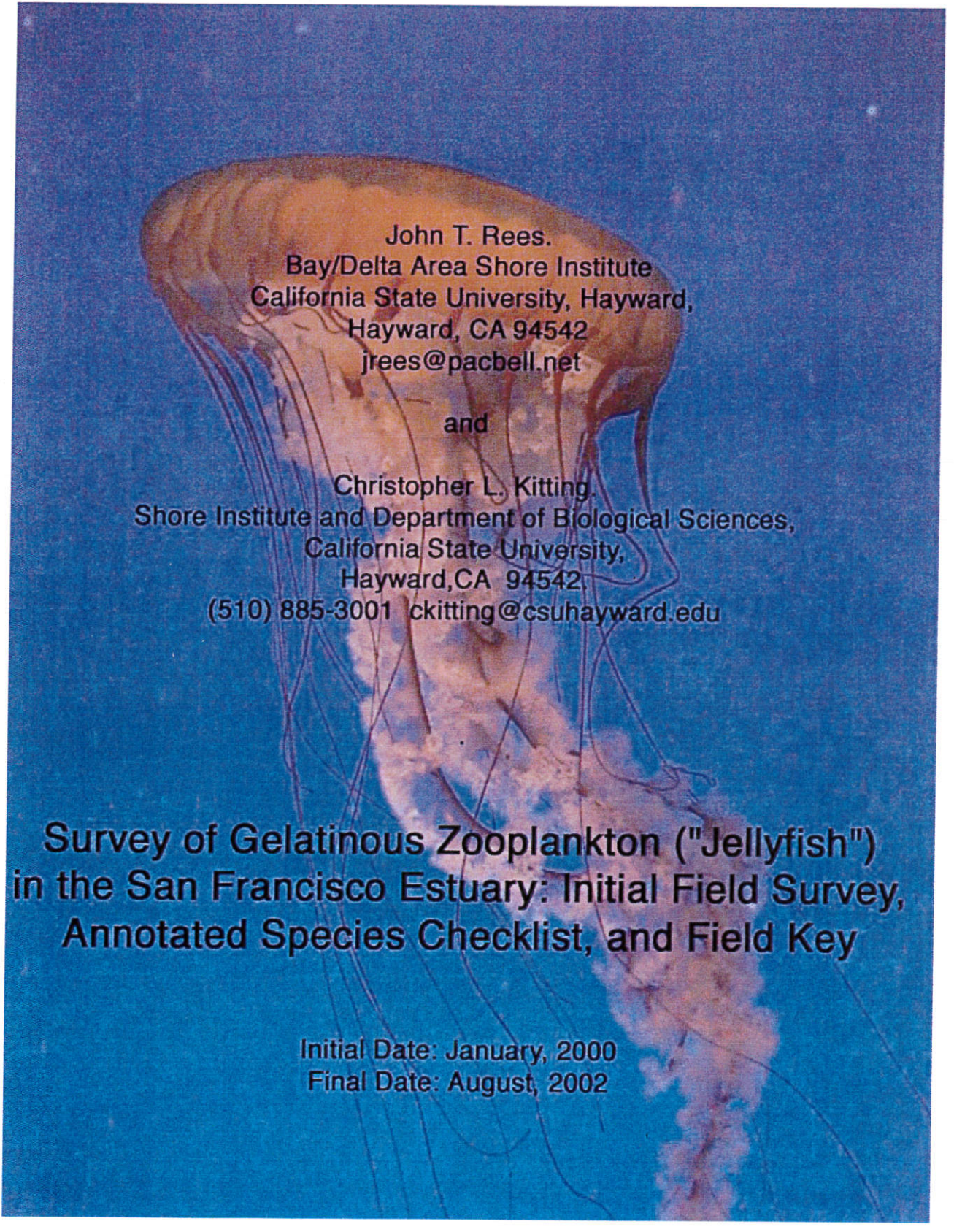
California Department of Fish and Game
U.S. Fish and Wildlife Service
U.S. Geological Survey
U.S. Environmental Protection Agency

National Marine Fisheries Service

Single copies of this report may be obtained without charge from:

State of California
Department of Water Resources
P.O. Box 942836
Sacramento, CA 94236-0001

If you need this publication in an alternate form,
contact the Division of Environmental Services Office at (916) 227-1375



John T. Rees.
Bay/Delta Area Shore Institute
California State University, Hayward,
Hayward, CA 94542
jrees@pacbell.net

and

Christopher L. Kitting.
Shore Institute and Department of Biological Sciences,
California State University,
Hayward, CA 94542.
(510) 885-3001 ckitting@csuhayward.edu

**Survey of Gelatinous Zooplankton ("Jellyfish")
in the San Francisco Estuary: Initial Field Survey,
Annotated Species Checklist, and Field Key**

Initial Date: January, 2000
Final Date: August, 2002

Table of Contents

Abstract.....	1
Introduction.....	1
Notes on Terminology.....	2
Methods.....	2
Field Sampling in 1999.....	2
Historical Records of Occurrence.....	4
Results.....	4
Distribution and Ecology of Native Jellyfish Species in 1999.....	4
Distribution and Ecology of Introduced Jellyfish in 1999.....	7
Population Densities and Relationship to Salinity in Introduced Jellyfish.....	10
Distribution of Native and Introduced Jellyfish Species in the Estuary in 1999.....	10
Further Results and Discussion.....	12
Acknowledgments.....	15
References.....	16
Notes.....	18
Appendix A.....	19
Annotated List of Estuary Jellyfish.....	19
Appendix B.....	23
Field Key to the Larger and More Commonly Encountered "Jellyfish" in the San Francisco Estuary.....	23
Illustrations of the Larger and More Commonly Encountered "Jellyfish" in the San Francisco Estuary.....	25
<i>Pleurobrachia bachei</i>	26
<i>Scrippsia pacifica</i>	27
<i>Polyorchis penicillatus</i>	28
<i>Maeotias marginata</i>	29
<i>Blackfordia virginica</i>	30
<i>Moerisia</i> sp.	31
<i>Aurelia aurita</i>	32
<i>Aurelia labiata</i>	33
<i>Chrysaora fuscescens</i>	34
<i>Pelagia colorata</i>	35
<i>Cyanea capillata</i>	36
<i>Phacellophora camtschatica</i>	37

Table

Table 1	Sampling sites and major jellyfish taxa detected in 1999.....	5
---------	---	---

Figures

Figure 1	Jellyfish sampling sites.....	3
Figure 2	Size classes of the most abundant jellyfish at Alameda Point.....	6
Figure 3	Population densities of jellyfish size-classes near the water's surface at Cuttings Wharf, Napa River, 1999.....	8
Figure 4	Population densities of jellyfish size-classes near the water's surface at Kennedy Park Launch, Napa River, 1999	9
Figure 5	<i>Blackfordia virginica</i> (#100/m ³) near the water's surface at Napa River compared with water temperature, May - October 1999	9
Figure 6	Population densities of jellyfish size-classes near the water's surface at Chipps Island, 1999	10
Figure 7	San Francisco Estuary major introduced jellyfish, by size class	11
Figure 8	Distribution of native and introduced jellyfish, San Francisco Estuary, 1999	11

Survey of Gelatinous Zooplankton ("Jellyfish") in the San Francisco Estuary

Abstract

This report presents results of a 1999 field survey of jellyfish in the San Francisco Estuary, along with an annotated species checklist and illustrated field key. The field survey compares salinity, temperature, and other environmental parameters with the predominance of native and introduced jellyfish in the estuary, with most data collected in the summer of 1999. The list and field key cover jellyfish species now present in the estuary.

In 1999, within the estuary, native and introduced jellyfish species clearly occurred in distinct geographic areas under different environmental conditions and tended to reach maximum abundances at different times of the year. Previous observations in 1998 showed higher jellyfish abundances with somewhat more distributional overlaps. Jellyfish abundances throughout the water column have been observed as patchy in both space and time, particularly in shallow water areas (≤ 2 m deep at low tide) over scales of kilometers and months.

Native species of jellyfish were found to inhabit marine reaches of the outer estuary, while exotic species have colonized and may complete their life cycle in the oligohaline areas of the upper estuary where no native jellyfish were originally known. Essentially no jellyfish occurred in extensively sampled shallow marsh habitats.

Introduction

Three groups of gelatinous plankton are included among the local "jellyfish": hydromedusae, scyphomedusae, and ctenophores. (A fourth group of jellyfish, the "box jellies," are not found in San Francisco Bay.) Hydromedusae and scyphomedusae are in the phylum Cnidaria, while ctenophores comprise their own phylum. With few exceptions, jellyfish are planktonic predators, feeding on zooplankton and small fishes. To capture prey, ctenophores utilize colloblasts (glue cells) rather than the nematocysts (stinging capsules) of cnidarians. Both hydrozoans and scyphozoans have complex life cycles consisting of benthic polyps and pelagic medusae, and both polyp and medusa of the same species can exist simultaneously in the field. Under field conditions not yet understood, asexual polyps develop and release very small (1 to 2 mm bell height) medusae, which subsequently develop in the plankton into sexually mature jellyfish. Hydrozoans release hydromedusae and scyphozoans release scyphomedusae. In contrast, ctenophores do not have complex life cycles and exhibit direct development from egg to adult.

The study of jellyfish ecology is in its infancy. Most jellyfish are marine, and the ecology of estuarine or brackish-water environments is not understood. Taxonomic treatments of the group, such as that of Russell's *Hydromedusae and Scyphomedusae of the British Isles* (1953, 1970), contain scattered ecological information such as time of year of occurrence and temperature and salinity in which particular species are found, but do not present comparative ecological data. More recently, Purcell and others (1999) showed that estuarine hydromedusa, *Moerisia lyonsi*, introduced to Chesapeake Bay, reached concentrations of about 14 jellyfish per liter in brack-

ish-water laboratory mesocosms, feeding primarily on copepods. A closely related species of *Moerisia* is now found in upper San Francisco Estuary.

A systematic survey of jellyfish within the San Francisco Estuary has not been undertaken previously; neither has a key nor checklist of estuary jellyfish been available. Foerster (1923) reviewed the hydromedusae of the Pacific coast, concentrating on Puget Sound in Washington. Arai and Brinkmann-Voss (1980) presented a very useful volume on the *Hydromedusae of Puget Sound*, and Wrobel and Mills (1998) published a beautifully illustrated *Guide to Pelagic Invertebrates of the Pacific Coast*. Both these volumes complement the field key presented in this report.

Mills and Sommer (1995) reported the first alien jellyfish in the San Francisco Estuary; two species of hydromedusae thought native to the Black Sea, *Maotias marginata* (formerly *M. inexpectata*) and *Blackfordia virginica*, were found in the Petaluma River from July through October 1993. *B. virginica* was also present in the Napa River in October of the same year. The first collection of *B. virginica* in the estuary was recorded in 1970 from the Napa River, misidentified as *Phialidium* (Cohen and Carlton 1995). *B. virginica* was collected again in the Petaluma River in 1974. A third introduced species, *Moerisia* sp., was found in Suisun Slough in 1997 and in the Napa River in 1998 (Rees and Gershwin 2000). Anecdotal evidence suggests that these three introduced jellyfish species have been observed in greater frequency and abundance over the past 10 years. This report provides a baseline for estuary jellyfish species now present and some of the environmental conditions (salinity, temperature, and turbidity) under which these jellyfish presently occur.

Notes on Terminology

To avoid confusion and repetition, we used the following terminology throughout this report. "Jellyfish" refers to three taxa: (1) hydrozoan medusae (cnidarian class Hydrozoa—generally smaller jellyfish, with a curtain-like velum around margin); (2) scyphozoans (class Scyphozoa—generally larger jellyfish, with a partitioned stomach); and (3) ctenophores (phylum Ctenophora—the comb jellies). An additional group of jellyfish, cnidarian class Cubomedusae, the "box jellies," are not found in San Francisco Bay.

The study area included estuarine habitats under tidal influence in San Francisco, San Pablo, and Suisun bays, and the outer Sacramento-San Joaquin Delta. This area is called the San Francisco Estuary, or "the estuary." "Outer Delta" refers to the area of the rivers' confluence, from roughly Chipps Island east to a line connecting Clifton Court Forebay, the Terminous Tract, and north to Courtland. "Upper estuary" refers to north San Pablo Bay and its sloughs, Suisun Bay and its sloughs, and the outer Delta. San Francisco Bay and southern San Pablo Bay comprise the "outer estuary." We define "Central Bay" as that area from the western tip of Alameda Island north to Pt. San Pablo in the east, west to the Bay Bridge terminous in San Francisco, and north to the Marin Islands and Gravel Pit Point in Marin County.

Methods

Field Sampling in 1999

As a broad initial assessment of jellyfish in the northern San Francisco Bay Estuary, sampling was undertaken on a transect from the Golden Gate to the Delta and included sites near Alameda and in the Napa River (Figure 1). Standardized plankton tows were undertaken approximately monthly from May through October in 1999 (before, during, and after seasons of introduced jellyfish), at permanent, accessible sampling sites at approximately 10-km intervals along the transect. The marsh locations were sampled monthly throughout the year. Tows near

all these sites were taken in other seasons, but less frequently. Additional sites not listed also were sampled, but less frequently. In such murky, current-swept water, with few points of access, any unintentional sampling bias for plankton was avoided, other than our bias against very rough water conditions. Moderate water turbulence introduced a random component into the sampling at each site. The sampling was not intended to generalize jellyfish population densities for the entire estuary. Arithmetic means of replicating samples at each site and date allowed clear, intuitive comparisons of approximate jellyfish abundances among very different sites, months, salinities, and temperatures. Nonparametric statistics were calculated with Statview 5 software (SAS Institute, Inc.). Temperature was measured with a portable temperature probe. Salinity was measured with a hand-held refractometer and YSI conductivity meter, and turbidity with a secchi disk.

Standardized plankton tows were conducted according to a pre-established protocol. Plankton data (especially on delicate jellies) are rarely optimal, but this initial sampling was designed for basic comparisons of major differences among sites and major jellyfish taxa. Duplicate or quadruplicate 20-minute tows (1.9 km through the water) were taken from a boat with two or four plankton nets (<0.28-meter mouths and 200 to 400 μ m mesh) simultaneously during midday. Thus, approximately four replicate tows near the surface of the water column (<0.5 m depth) were conducted on each date at each site. Sample volumes were estimated by towing samples crosscurrent between two fixed lines (via dGPS), or by towing for equal times up and down current during each tow. Effective distances sampled through the current were determined with a sea anchor and survey tape to calculate the speed of the net through the water, adjusting tow time accordingly. (Our General Oceanics flow meter was less reliable at towing speeds.) Each replicate sample thus totaled a volume of $\sim 100 \text{ m}^3$ ($= \pi r^2 \times \text{distance through water}$). Shore-based sampling, totaling about 2 m^3 , was conducted with 1-mm mesh set in a customized 0.8 x 0.8-m frame, and with plankton nets towed by hand. Surface tows enabled comparisons with shallow-water sites and previous sampling, and with measured water clarity.

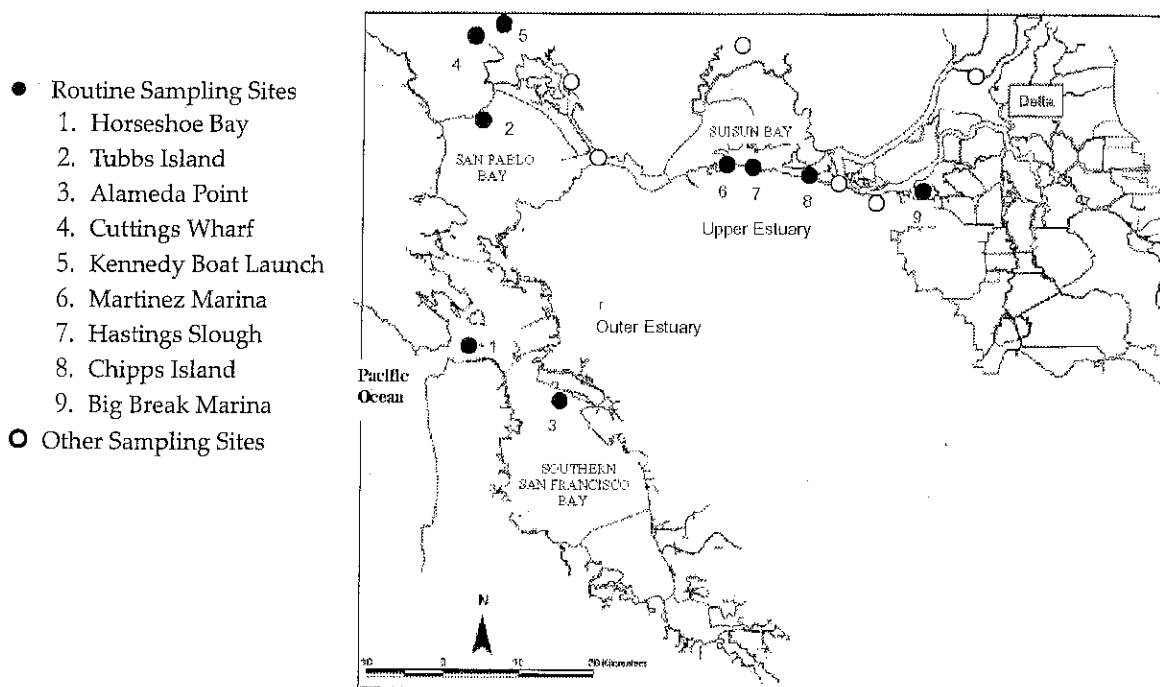


Figure 1. Jellyfish sampling sites

To detect jellyfish throughout the entire water column, 1 mm-mesh, flat-bottomed pool nets were used periodically to supplement the above samples. These nets enabled sampling along the bottom or at any chosen depth. Such supplemental data were not averaged with the standardized surface samples. Only surface samples were used for comparisons through time or region. Additional sampling was used to confirm cases of low jellyfish abundance.

In each sample in the field, medusae were identified and counted by size class (down to a minimum size of 4 mm bell width). Magnification and supplemental lighting were employed as needed. Larval and juvenile fish taken in samples also were noted and returned to the water. Subsamples and specimens of questionable identification were returned to the laboratory for further examination. A 24-hour supplemental sampling was conducted September 2 through 3, performed every 4 hours over the tidal cycle to determine if timing of the tidal or diel cycle influenced dense jellyfish (in this case, *B. virginica*) abundance.

Historical Records of Occurrence

Records of jellyfish in the Estuary in years prior to 1997 were gleaned from a number of sources including: (1) specimens sampled by the authors, especially from 1995-1998; (2) preserved specimens in other collections such as those at the California Academy of Sciences; (3) notes from Bay-Delta fish survey sheets from the California Department of Fish and Game (DFG) and U.S. Fish and Wildlife Service (USFWS); and (4) oral communication from a variety of personnel, including DFG and USFWS staff (Stockton and Sacramento offices), the California Department of Water Resources' staff (Sacramento), marina owners and operators, fishermen, and other colleagues.

Results

Distribution and Ecology of Native Jellyfish Species, Particularly in the 1999 Survey

Native jellyfish species occurred primarily in fall, winter, and early spring. Maximum population abundances of natives occurred from December 1998 through February 1999. Table 1 summarizes sampled locations and conditions corresponding to each common jellyfish species.

Polyorchis penicillatus

In 1999, *P. penicillatus* was present at both outer Estuary sites at Alameda and Horseshoe Cove, and nearby. *P. penicillatus* was present at Alameda Point from January through March 1999, and November 1999 through May 2000. It was common around the ship piers and shallow-water marina of the Seaplane Lagoon. Increases in size cohorts within populations of *P. penicillatus* at Alameda Point were clearly evident over a 6-week period from November to January 2000, suggesting a growth rate of about 1 cm per month (Figure 2).

P. penicillatus was found in cool (12 to 17 °C) and clear (100 to 600 cm Secchi depth) water at salinities ≥ 20 ppt. In 1999, maximum summer densities of *P. penicillatus* at Horseshoe Cove near the Golden Gate occurred in August, with approximately 0.7 individuals per m³ at the surface. Medusae appeared concentrated downwind. At Alameda, the medusae were observed feeding on swarms of copepods at the surface. Concentrations of 1 medusa per m³ at the surface were measured during times of maximum abundance.

Table 1. Sampling sites, including any major jellyfish taxa detected in 1999, and the corresponding conditions

Sampling Location	Coordinates	Jellyfish Species Present	Peak Season	Temp. with Jellyfish	Salinity with Jellyfish	Water Clarity (Secchi)
<i>Central and North Bay:</i>						
*Horseshoe Bay (at Golden Gate)	37° 50.0' N 122°28.4' W	<i>Polyorchis penicillatus</i> ^(†)	wint-sum	12-15 °C	≥20 ppt	200 cm
*NW of Alameda Point & Alameda Point piers	37° 46.9' N 122°20.2' W	<i>P. penicillatus</i> ; ctenophore <i>Pleurobrachia bachei</i> ^(†)	wint-spr	14-17 °C	>23 ppt	~300 cm
*Tubbs Island Marsh (N. San Pablo Bay)	38° 07.2' N 122°26.2' W	None				
<i>Napa River:</i>						
Napa River Mouth (13 km S of Cuttings Wharf)	38° 04.6' N 122°14.7' W	None				
Midway btw Napa River Mouth and Cuttings Wharf	38° 11.2' N 122°18.7' W	None				
*Cuttings Wharf	38° 13.6' N 122°18.45' W	<i>Blackfordia virginica</i> ^(‡)	Aug-Sept	18-22 °C	10-16 ppt	30-50 cm
Midway btw Cuttings Wharf and Kennedy Park	38° 14.8' N 122°17' W	<i>Blackfordia virginica</i>				
*Kennedy Boat Launch	38° 15.9' N 122°17' W	<i>Blackfordia virginica</i>	Aug-Sept	20-24 °C	7-13 ppt	25-50 cm
7 km upriver of Kennedy Park	38° 19.5' N 122°16.6' W	None				
<i>Suisun Bay:</i>						
Martinez Marina	38° 01.6' N 122°08.2' W	<i>Moerisia</i> sp. ^()	Aug-Sept	13-22 °C	8-15 ppt	40-55 cm
*Hastings Slough (Pt Edith)	38° 03.0' N 122°03.5' W	<i>Oreomastix marginata</i> ^(‡)				
Suisun City Marina	38° 14.2' N 122°02.2' W	<i>Maeotias marginata</i>	Sept-Oct	18-20 °C	4-6 ppt	24-30 cm
McAvoy (Pittsburg)	38° 02.4' N 121°57.4' W	None				
Chippis Is (Spoonbill Slough)	38° 03.2' N 121°53.8' W	<i>Maeotias marginata</i>	Sept-Oct	18-23 °C	4-6.5 ppt	30-50 cm
Pittsburg Marina	38° 02.5' N 121°53.2' W	None				
<i>Outer Delta:</i>						
SW Brannon Island	38° 06.9' N 121°41.2' W	<i>Maeotias marginata</i>	Sept	~20 °C	~1 ppt	~60 cm
Big Break Marina	38° 01.2' N 121°43.9' W	None				

Note: Sites are arranged by distance from Golden Gate to the Delta. In sites with (*), approximately monthly tows were taken from May through October. All sites were sampled throughout the year. Jellyfish common at each location are noted: native species (+); introduced species (‡). Noted conditions represent those in which jellyfish were most abundant.

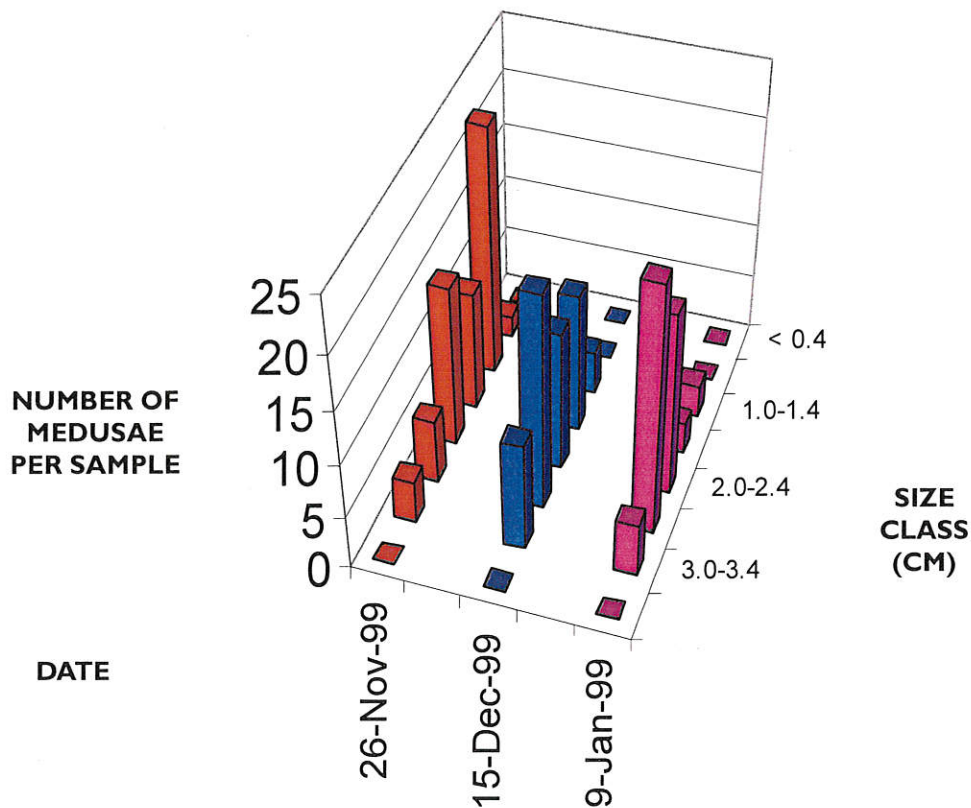


Figure 2. Size classes (measured as bell height) of an abundant jellyfish at Alameda Point, *Polyorchis penicillatus* (a native) throughout its peak abundance.

Scrippisia pacifica

Two juveniles of this large hydromedusa were sampled at Alameda in December 1999 and January 2000. Water temperature was 11.5 to 12.5 °C and salinity, 32 to 34 ppt.

Pleurobrachia bachei

This native ctenophore appeared at the same time as *P. penicillatus* at Alameda and appears to have similar environmental requirements of temperature and salinity. It was observed feeding on copepods around pier pilings. Previously, it has not been reported as a brackish water species, but during the survey was collected at salinities as low as 23 ppt. Population densities of this species reached approximately four individuals per m³ at the surface at Alameda, the highest concentration of any native jellyfish surveyed in 1999.

Aurelia labiata (moon jelly)

This scyphozoan was observed once at Alameda on December 6, 1999. Temperature was 12.5 °C and salinity, 32 ppt. Specimens of what may have been this species were taken "in abundance" in oblique fish trawls from September through November 1999 in San Pablo Bay (R. Gartz, personal communication). Adults are common in the outer estuary in late summer and early fall.

Distribution and Ecology of Introduced Jellyfish Species in 1999

Two of the three introduced jellyfish found in the upper Estuary, *Blackfordia virginica* and *Maeotias marginata*, became abundant in open water during late summer and early fall 1999. These common introduced species were found at salinities and locations distinct from one another during 1999 (Table 1). Estuarine jellyfish (predominantly introduced species) were patchy overall, with a mean population density of 0.40 per 10 m³, ± 1.7 std. dev. ($N = 93$ standardized surface samples).

Blackfordia virginica

Except for one specimen sampled at Chipps Island, *B. virginica* was detected only in the Napa River samples in 1999. The medusae first appeared in the plankton in mid-August and remained until early September (Figures 3, 4). Within 2 weeks, all macroscopic size classes appeared, and persisted for a month. Cuttings Wharf, closer to the bay and with higher salinity, yielded more and larger *B. virginica* (Figure 3) than did Kennedy Park, 4 km upstream (Figure 4; Wald-Wolfowitz Runs Test, $N = 35$, $Z = 3.4$, $P = 0.0007$). By early October, the medusae had disappeared (Figures 3, 4). *B. virginica* medusae were first detected when salinities had risen to 17 - 20.5 ppt at Kennedy Boat Launch and Cuttings Wharf on August 12. The appearance of the medusa was associated with increasing salinity, and medusae became abundant in salinities ranging from 6.5 to 16 ppt and variable but warm water temperatures (20 to 24 °C; Figure 5). Maximum surface population densities reached about 1 medusa per 10 m³. Simultaneously sampled bottom populations were estimated to be more dense, up to approximately 5 per m³, although this deep sampling normally was not conducted.

Salinity was seen to be spatially as well as temporally associated with abundant *B. virginica*. In the Napa River, a salinity gradient was present throughout the season. Salinities decreased in a gradient upstream from Cuttings Wharf to the City of Napa. A transect sampled during August showed *B. virginica* to be associated with a salinity range of 6.5 to 16.0 ppt, in the area between Cuttings Wharf and Kennedy Boat Launch (Table 1).

The size distribution of abundant medusae on September 2 at Cuttings Wharf showed all size classes present in the population, indicating that the hydroid phase was releasing medusae at this time, late in the animal's peak abundance (Figure 3). Those temperatures of 20 to 21 °C and salinities of 13 to 14 ppt must be suitable for release of *B. virginica* medusae from the parent hydroid. One specimen of *B. virginica* was sampled at Chipps Island on September 7, in salinities of 5.5 ppt and temperatures of 21 °C. Water clarity was low whenever *B. virginica* was present (27 to 50 cm Secchi depth).

Maeotias marginata

In 1999, *M. marginata* was present at the Chipps Island and Suisun Slough sampling sites. Medusae were detected in September and October, but not in July and August (Figure 6). Maximum densities attained were about 0.6 medusae per 10 m³. Environmental parameters were similar at both sites when medusae were present: low salinity (3.7 to 5.8 ppt), temperatures ranging from 17.7 to 22.5 °C, and low water clarity (24 to 30 cm). At other sampling sites (without *M. marginata*) at least one of these three parameters fell outside these ranges.

As earlier in the year with *B. virginica* (Figures 3, 4), the presence of small medusae in population profiles of *M. marginata* on September 7 at Chipps Island (Figure 6) confirmed that conditions of 20.9 °C temperature and 5 to 6 ppt salt are suitable for release of medusae from the parent

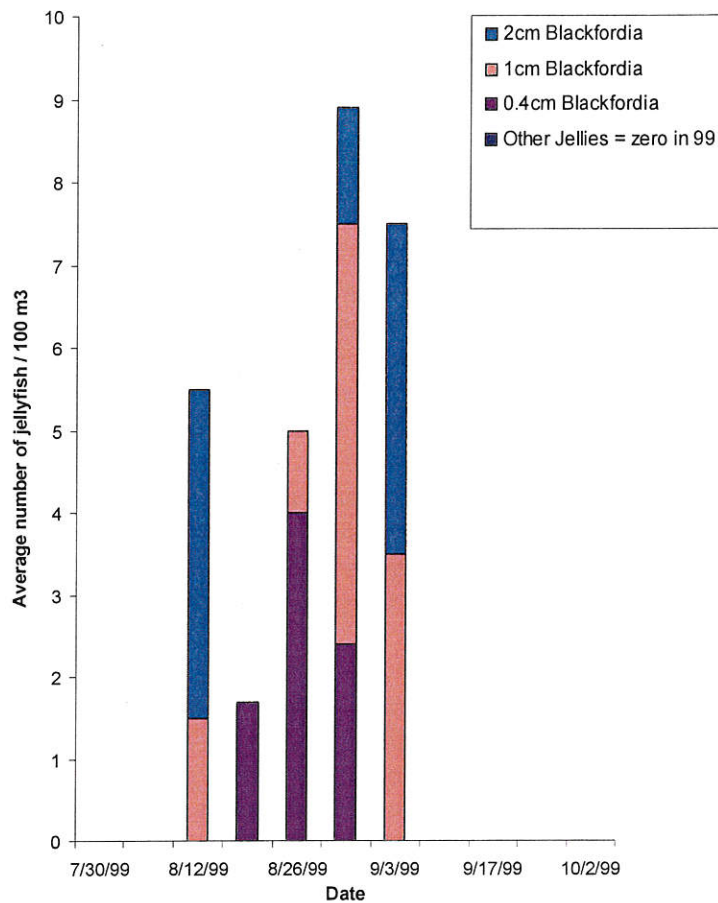


Figure 3. Population densities of jellyfish size-classes near the water's surface at Cuttings Wharf, Napa River, 1999. (Only *Blackfordia virginica* was present.) Sample dates before and after jellyfish abundance yielded no jellyfish.

hydroid. In later September, large *M. marginata* were sampled at lower salinities (about 1 ppt) further up into the Delta, near Brannon Island on the San Joaquin River. In contrast, *M. marginata* was not seen at all at Big Break, at slightly lower salinities about 10 km south of Brannon Island, and about 10 km east of the confluence of the Sacramento and San Joaquin rivers.

Moerisia sp.

The medusa of this species was detected only three times in 1999, at Cuttings Wharf in the Napa River on August 20, and at the Martinez Marina in August and September. Salinities were 13 to 16 ppt, temperatures 13 to 22 °C, and water clarity, 40 to 55 cm. In 1998, *Moerisia* was collected in the Napa River at salinities of nearly 8 ppt, temperatures of 23 °C, and water clarity of about 7 cm. In 1997, this species was abundant (≥ 1 medusa per m^3) in Suisun Slough in October, at 18 °C and salinities of about 15 ppt.

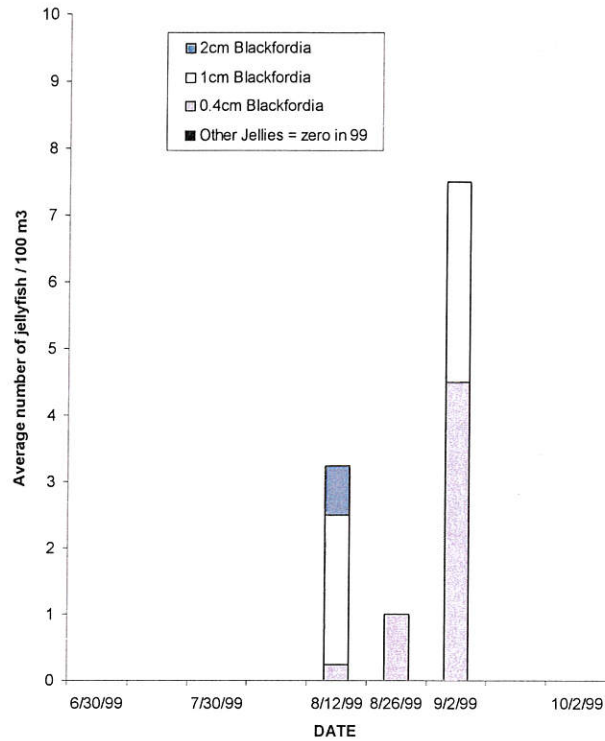


Figure 4. Population densities of jellyfish size-classes near the water's surface at Kennedy Park Launch, Napa River. (Only *Blackfordia virginica* was present.) Sample dates before and after jellyfish abundance yielded no jellyfish.

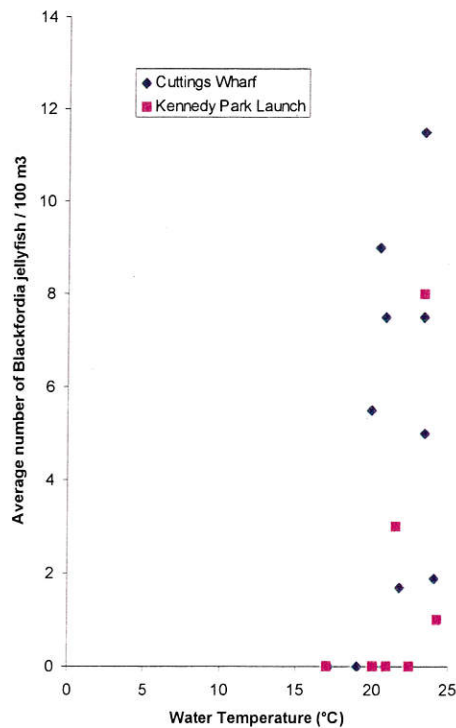


Figure 5. *Blackfordia virginica* jellyfish (#100/m³) near the water's surface at Napa River compared with water temperature, May - October 1999. Lower temperatures elsewhere had no detectable *B. virginica*.

Population Densities and Relationship to Salinity in Introduced Jellyfish

Introduced jellyfish attained their highest 1999 densities in early September both at the Napa River (*B. virginica*) (Figures 3, 4) and Chipps Island sites (*M. marginata*; Figure 6). Maximum average abundances attained near the bottom were about 50 jellyfish per 100 m³ for both species. Maximum abundances for *B. virginica* were attained in salinities about 14 ppt, and for *M. marginata*, about 5 ppt (Figure 7). Based on standardized tows near the surface, abundances of each common introduced jellyfish, *M. marginata* and *B. virginica*, differed significantly from the major sampled sites with the most jellyfish: Napa River and Chipps Island sites ($N = 56$ standardized samples, Mann-Whitney U' about 500, $P < 0.015$).

Distribution of Native and Introduced Jellyfish Species in the Estuary in 1999

Figure 8 illustrates a generalized distribution of native and introduced jellyfish in the estuary, particularly during 1999. Native jellyfish occurred in the outer estuary much of the year, while introduced jellyfish occurred in the upper estuary, primarily in summer through fall. Such observations were consistent with previous and subsequent years of observations.

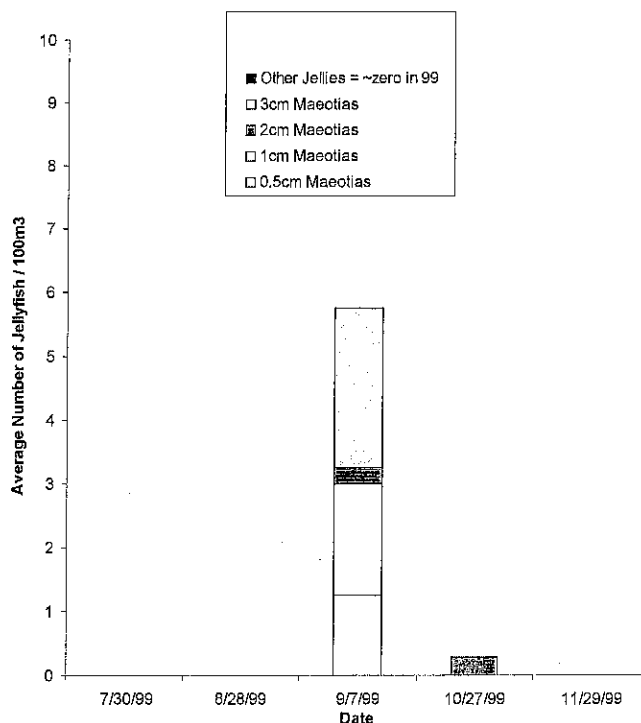


Figure 6. Population densities of jellyfish size-classes near the water's surface at Chipps Island, 1999. (Essentially all were *Maeotias marginata*.) Sample dates before and after jellyfish abundances yielded no jellyfish.

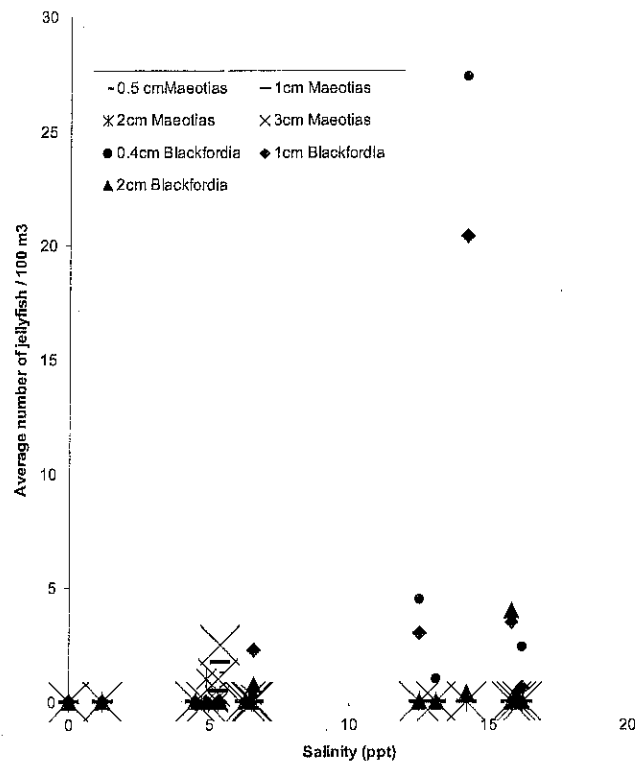


Figure 7. San Francisco Estuary major introduced jellyfish, by size class. Average population densities v. salinity are compiled throughout the water column, Napa River and Chipps Island, 1999.

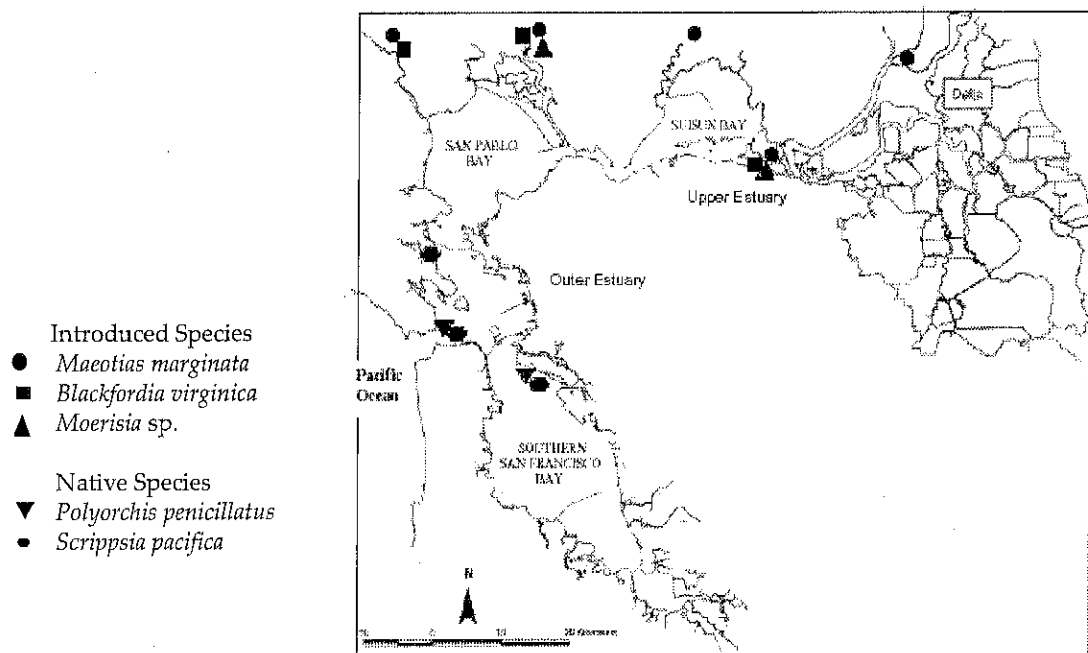


Figure 8. Distribution of native and introduced jellyfish in the San Francisco Estuary during 1999.

Further Results and Discussion

Results of field sampling in 1999 showed that even this initial, basic sampling illustrates that the distribution of native and introduced jellyfish species in the estuary fell into two distinct geographic areas: (1) native jellyfish were found in the more saline outer estuary of San Pablo and San Francisco bays (Rees and Kitting 2000), and (2) introduced jellyfish were found in the oligo-to-mesohaline parts of the upper estuary, including Suisun Bay, the outer Delta, and the Napa and Petaluma rivers. Introduced hydromedusae in the upper estuary are all warm water oligo-to-mesohaline species, completing their life cycles in turbid (≤ 40 cm), warm (≥ 17 °C) water of variable salinity (1 to 17 ppt), depending on the species. In contrast, the native jellyfish of the outer estuary, were found in cool (≤ 17 °C), relatively clear (> 50 cm) and relatively non-variable salinity (≥ 20 ppt) water, conditions found in embayments up and down the California coast without large freshwater inputs. The relatively large, warm, variable-salinity water of Suisun Bay and north San Pablo Bay is unique in Central and Northern California, and provides conditions similar to that in the Black and Caspian seas during the summer months where these introduced hydromedusae are believed native. Especially if ballast water is a probable origin of recently accelerated species invasions (Cohen and Carlton 1995), either the alien jellyfish polyps, or medusae, or both, probably were released into the waters of the upper estuary during warm water periods from late spring to late fall. Possibly, the presence of native, widespread jellyfish in more marine areas of the outer estuary has precluded more jellyfish introductions there. We can predict that one or more of the introduced jellyfish now present in the upper estuary will invade other areas where suitable environmental conditions of high temperatures and moderate and variable salinities are present.

Jellyfish populations are known to be patchy, which can hinder estimates of overall population densities. Concentrations of jellyfish encountered in the field, known as jellyfish "blooms," may actually be the result of physical environmental conditions, such as currents or wind. Such extreme patchiness was not evident in these 1999 samples. Densities of jellyfish near the surface in the upper estuary in 1999 averaged up to about 1 per 10 m³ (*B. virginica*, Napa River in September). We suspect that jellyfish population densities in 1999 were lower and developed later in the year than usual due to low spring temperatures, late rains, and a generally cool summer that year. In late August 1998, we sampled *Blackfordia virginica* populations at Cuttings Wharf between 2 and 3 medusae per m³ in temperatures of 27.0 °C. These high temperatures were not observed in the Napa River in 1999 (sampled at a maximum of 24.2 °C). *Maeotias marginata* also was common in the Napa River in 1998 (Rees 1999), but were rarely detected there in 1999. Moore (1987) reported high population densities for *B. virginica* (about 47 per m³) in estuaries on the western coast of India, and 67 per m³ in the Mira Estuary, SW Portugal. These high densities might also develop in the San Francisco Estuary. The role of higher temperatures (25 to 30 °C) in the population explosions of these introduced estuarine jellyfish is not known.

In field samples, we did not attempt to count medusae smaller than 0.4 cm in diameter. Subsamples examined at higher magnification in the laboratory revealed that our field methods did not detect jellyfish < 0.3 cm in diameter. As in 1998, our 1999 sampling showed that *B. virginica* medusae < 0.3 cm in diameter were abundant when larger medusae were present. Such a population profile indicates that *B. virginica* hydroid colonies were releasing medusae rapidly. Newly released hydromedusae are tiny, usually ≤ 1 mm in bell height, and are easily overlooked. Methods are being improved to assess the range of jellyfish size classes in the field so as to obtain data on population structure and total density.

Results of supplemental small-scale sampling in 1999 indicated that *B. virginica* was more abundant deeper in the water column than at the surface. When surface tows detected no jellyfish, deeper samples confirmed few to no jellyfish. In addition, sampling throughout a 24-hour period when *B. virginica* was abundant suggested similar *B. virginica* abundances throughout the diel cycle. Our standard samples near the surface probably yield minimum jellyfish population densities. Replicate samples showed variability. However, re-sampling when jellyfish populations were most abundant (*B. virginica* at Napa River sites) suggested consistent average abundances (mean = 4.75 jellyfish per 10 m³, + 4.98 std. dev. N = 8 replicate samples, where a coefficient of variation = std. dev./mean = 1.05, suggesting a random, normal distribution locally). Month-to-month samples sometimes showed major changes in jellyfish abundance for all size classes at a given site, suggesting rapid growth in bell size and abundance, and rapid declines.

With one exception, jellyfish were not found in our shallow water (< 2 m depth) marsh sites with emergent vegetation, including marsh tidal creeks near the Napa River and in southern Suisun Bay during 1999. One 2-cm *M. marginata* turned up in a very large volume (> 5,000 m³) sample in a tidal creek of Hastings Slough (southern Suisun Bay) on December 1, 1999, at 10.5 ppt salinity and 12.4 °C. Even during peak abundances of *M. marginata* near Chipps Island, populations were not detected along nearby shorelines of southern Suisun Bay. Jellyfish might not survive in shallow-water marsh habitats because tidal currents and emergent vegetation could damage medusae, as we observed these medusae becoming abraided in aquaria in the field. Supplementary observations have detected common ctenophores (*Pleurobrachia*) occasionally in San Pablo Bay marshes.

Larval and other small fishes were present in standardized samples, but were far less abundant than introduced jellyfish. Laboratory observations suggested that these introduced jellyfish have a relatively mild sting, and were observed to kill fishes only smaller than the jellyfish. Mills and Sommer (1995) reported that *Maeotias marginata* consumed small planktonic crustaceans. Purcell and others (1999) showed that *Moerisia* sp. fed on copepod nauplii and adults in laboratory mesocosms. Feeding habits of *Blackfordia virginica* are not known. Knowledge of jellyfish population structure, distribution, and limiting factors is scanty (Purcell 1992, 1997). Both jellyfish and their attached benthic polyp stages have been shown to deplete zooplankton populations in controlled mesocosms (Purcell and others 1999). Medusae were capable of consuming up to 64 nauplii per liter with no prey saturation. *M. marginata* and *B. virginica* are medusae larger than *M. lyonsi*, and presumably feed on larger prey. Further work on food habits of estuary jellyfish, particularly on the introduced species, is needed.

Dates of initial introductions of the three introduced jellyfish species in the upper estuary can only be surmised through examination of available records and discussions with field workers. *Maeotias marginata* apparently has been present in the estuary since 1961, when "gallons" of jellyfish (according to notes on DFG data sheets) were collected in the lower Sacramento River during a DFG Summer Trawl Survey (S. Foss, personal communication). These were probably *M. marginata*, given what we know now about the adult size, population distribution, and salinity tolerances of this species. *Blackfordia virginica* has been present since at least 1970, as this species was collected in the Napa River that year, based on specimens of misidentified jellyfish (as *Phialidium* sp.) in the California Academy of Sciences collections. *Moerisia* sp. has been present in the estuary since at least 1993, when polyps of this species were collected (Mills and Sommer 1995; Mills and Rees 2000). Estimated times of introduction of these three hydrozoan exotics—1961, 1970, and 1993—intimates a recent and rapid sequential introduction of a group of planktonic predators, which now occupy a niche not formerly filled in the upper estuary. The establishment of these species in this fisheries nursery area provides a strong argument towards prevention of further invertebrate introductions into the estuary.

The list of estuary jellyfish presented in this report establishes a baseline for jellyfish species now common in both the upper and outer estuary, and, in conjunction with the field key, can be used to determine new jellyfish introductions and major changes in relative abundances of species of jellyfish now present. Other aggressive brackish water jellyfish species, e.g., the hydromedusa *Nemopsis* and the ctenophore *Mnemiopsis*, have become established in other estuaries with a high level of commercial and recreational boat traffic—*Nemopsis bachei* in the Loire estuary (Denayer 1973) and *Mnemiopsis leidyi* in the Black Sea (Harbison and Volovik 1994). Unless steps are taken to prevent further introductions, eventual establishment of these (and other) alien jellyfish species within the estuary is very likely.

A better understanding of the ecological role that jellyfish now play in the estuary, particularly the introduced species in the upper estuary, will only be forthcoming with further field and laboratory work. Of particular importance are diet and feeding rates of medusae in the field, temperature, salinity, and turbidity tolerances of polyps and medusae in the field and laboratory, and reproductive and survival rates of polyps and medusae under optimal and suboptimal conditions, including marsh habitats that may largely exclude or otherwise reduce jellyfish abundances in marshes. Of particular importance is an understanding of the factors that contribute to the development of high jellyfish population densities ("blooms"). The year 1999 did not yield particularly high jellyfish densities, compared with previous years. Evidence suggests blooms of *M. marginata* developing in Suisun Slough in 1997 and in the outer Delta in 1961 (S. Foss, personal communication). Under such conditions, jellyfish could have negative effects on zooplankton, zoobenthos, and ultimately on fish populations. A combination of ecological conditions might allow blooms to develop, including suitable conditions of temperature, salinity, turbidity, and food supply. Optimal conditions present during blooms would result in large numbers of jellyfish being released from hydroids, rapid growth of jellyfish, and presence of favorable hydrological factors, such as currents, winds, and/or salinity gradients concentrating jellyfish in the water column.

The outer estuary historically has harbored jellyfish species found along the open West Coast, a few of which can tolerate somewhat lower salinity (e.g., the hydromedusa *Polyorchis penicillatus* and the ctenophore *Pleurobrachia bachei*). However, native meso-to-oligohaline estuarine jellyfish species apparently have been absent in the upper San Francisco Estuary. Because jellyfish fill an ecological niche similar to larval and juvenile fish in aquatic food webs, jellyfish can be competitors with and consumers of native fish species. Jellyfish can compete directly with young fish for zooplankton (Purcell 1985). The effects jellyfish can inflict on aquatic ecosystems can be substantial, particularly when introduced into new areas. In the early 1980s, the ctenophore *Mnemiopsis leidyi* (Leidy's comb jelly), native to estuaries on the East Coast of the United States, appeared in the Black Sea, apparently introduced through ship ballast water discharge. Populations of this ctenophore developed into one of the most intense marine invasions ever recorded, nearly wiping out anchovies and other fisheries in the Black Sea and the Sea of Azov (Harbison and Volovik 1994). The potential threat to the San Francisco Estuary from this and other introduced jellyfish species warrants further investigation and prevention.

While evidence is scant and data difficult to interpret, several jellyfish populations recently were reported increasing in areas where commercial fish stocks have been seriously depleted by overfishing, such as the Bering Sea (Mills 1995). Jellyfish may be filling the niche vacated by formerly more abundant fish populations. In the Grand Banks, both normally benthic hydrozoan populations and hydromedusan populations have been recorded in high abundances in the plankton, and direct observations have been made of their feeding directly on larval cod (Bollens, personal communication). Whether these hydrozoan populations will decrease in response to increased

cod populations is not yet known. Potential impacts of jellyfish species on native fish species are a concern, particularly when native fish are declining in abundance due to environmental degradation and a generally diminished estuarine nursery environment.

Coelenterates were not native to the plankton of the upper estuary. San Francisco Estuary is geologically young (Conomos 1979), and no old estuarine environments, such as are found on the East and Gulf coasts of the United States, are found on the geologically-active West Coast. As a result, a niche for predatory gelatinous plankters largely was empty in the meso-to-oligohaline upper estuary, a niche historically filled in older estuarine environments, including the Black and Caspian seas with three native species of hydromedusae, and Chesapeake Bay, with at least one native ctenophore, *Mnemiopsis* (Caspers 1957; Harbison and Volovik 1994). Further introductions of alien jellyfish into the estuary are to be avoided.

Acknowledgments

We thank the following for their help with this project: Big Break Marina of DuPont Chemical and Martinez Bait and Tackle provided marina facilities; Chris Pattison, Karen Evans, and Edmund Duarte of CSUH, Terry Peard and Jason Blair from the Biology Department, Indiana University of Pennsylvania, and Lisa-Ann Gershwin from the Department of Integrative Biology, University of California, Berkeley, assisted in August jellyfish sampling; Freya Sommer of Hopkins Marine Station and Gershwin aided in jellyfish taxonomy; Terry Smith and Sara Webster assisted in presenting many of the graphs; Jeff McLain, Steve Foss, and Russ Gartz of the California Department of Fish and Game, Bay-Delta Division, provided supplemental information from DFG trawls; CALFED, U.S. Fish and Wildlife Service, San Pablo Bay National Wildlife Refuge, Contra Costa Mosquito and Vector Control, and Delta Science Center provided opportunities to sample marshes; Jeff McClain, Russ Gartz, Jim Orsi, other DFG personnel, and Lenny Grimaldo (California Department of Water Resources) provided helpful editorial advice. Our gratitude also goes to Randy Brown and Zach Hymanson (DWR and Interagency Ecological Program), who helped arrange funding and encouraged completion of much of this work.

References

- Arai MN, Brinckmann-Voss A. 1980. Hydromedusae of British Columbia and Puget Sound. Bulletin 204. viii + 192 p.
- Calder D. 1971. Hydroids and hydromedusae of the Chesapeake. Virginia Institute of Marine Science Special Papers in Marine Science 1:xi + 107 p.
- Caspers H. 1957. Black Sea and the Sea of Azov. In: Hedgpeth J, editor. Treatise on Marine Ecology and Paleontology, Volume I. Ecology. p 801-889.
- Cohen A, Carlton J. 1995. Nonindigenous aquatic species in a United States Estuary: a case study of the biological invasions of the San Francisco Bay and Delta. United States Fish and Wildlife Service, Washington, D.C., and the National Sea Grant Program Report No. PB96-166525. 246 p + appendices. Available from the National Technical Information Service.
- Conomos TJ. 1979. San Francisco Bay: the urbanized estuary. Pacific Division, AAAS. 493 p.
- Denayer JC. 1973. *Trois meduses nouvelles ou peu connues des cotes francaises: Maeotias inexpectata* Ostourmov, 1896, *Blackfordia virginica* Mayer, 1910, and *Nemopsis bachei* Agassiz, 1849. Cah Biol Mar 14:285-94.
- Eschscholtz F. 1829. *System der Acalephen. Eine ausführliche Beschreibung aller medusenartigen Strahltiere*: 1-190. Berlin: Ferdinand Dümmler.
- Foerster RE. 1923. The hydromedusae of the west coast of North America, with special references to those of the Vancouver Island region. Contrib Canadian Biol NS 1:221-77.
- Greenberg R, Garthwaite L, Potts DC. 1996. Allozyme and morphological evidence for a newly introduced species of *Aurelia* in San Francisco Bay, California. Mar Biol 125:401-10.
- Hand C. 1954. Three Pacific species of "Lar" (including a new species), their hosts, medusae, and relationships (Coelenterata, Hydrozoa). Pacific Science 8:51-67.
- Harbison GR, Volovik SP. 1994. The ctenophore, *Mnemiopsis leidyi*, in the Black Sea: a holoplanktonic organism transported in the ballast water of ships. In: Proceedings of the National Oceanic and Atmospheric Administration Conference and Workshop on Nonindigenous Estuarine and Marine Organisms. Washington, D.C.: U.S. Government Printing Office. p 25-36.
- Mayer AG. 1910. Medusae of the World. Vols I and II: The Hydromedusae. Carnegie Institute of Washington. 498 p.
- Mills CE. 1995. Medusae, siphonophores, and ctenophores as planktivorous predators in changing global ecosystems. ICES J Mar Sci 52:575-81.
- Mills CE, Sommer F. 1995. Invertebrate introductions in marine habitats: two species of hydromedusae (Cnidaria) native to the Black Sea, *Maeotias inexpectata* and *Blackfordia virginica*, invade San Francisco Bay. Mar Biol 122:279-88.

- Mills CE, Rees JT. 2000. New observations and corrections concerning the trio of invasive hydromedusae *Maeotias marginata* (= *M. inexpectata*), *Blackfordia virginica*, and *Moerisia* sp. in the San Francisco Estuary. *Scientia Marina* 64(Suppl 1):151-5.
- Modeer A. 1791. *Tentamen systematis medusarum stabiliendi*. Nova Acta Phys. Med. Acad. Leopold Carol. Nat. Cur. Tom. 8 App. No. 6. p 19-34.
- Moore SJ. 1987. Redescription of the leptomedusan *Blackfordia virginica*. *J Mar Biol Assoc UK* 67:287-91.
- Naumov DV. 1955. Hydroids and hydromedusae of the USSR. *Izd. Akad. Nauk USSR* 70:1-660. (Translated from Russian by Israel Prog. Sci. Transl. Jerusalem, 1969.)
- Purcell JE. 1985. Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. *Bull Mar Sci* 37:739-55.
- Purcell JE. 1992. Effects of the predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay. *Mar Ecol Prog Ser* 87:65-76.
- Purcell JE. 1997. Pelagic cnidarians and ctenophores as predators: selective predation, feeding rates, and effects on prey populations. *Ann Inst Oceanogr Paris* 73:125-37.
- Purcell JE, Bamstedt U, Bamstedt U. 1999. Prey, feeding rates and asexual reproduction rates of the introduced oligohaline hydrozoan *Moerisia lyonsi*. *Mar Biol* 134:317-25.
- Rees JT. 1999. Non-indigenous jellyfish in the Upper San Francisco Estuary: Potential impact on zooplankton and fish. *IEP Newsletter* 12(3):46-50.
- Rees JT. 2000. A pandeid hydrozoan, *Amphinema* sp., new and probably introduced to central California: life history, morphology, distribution, and systematics. *Scientia Marina*. (in press).
- Rees JT. Forthcoming. Environmental stress and the significance of the sessile colony in the maintaining the hydrozoan life cycle: life history and ecology of *Sarsia vesicularis* n. sp. in San Francisco Bay.
- Rees JT, Kitting CL. 2000. Seasonal comparison of introduced gelatinous zooplankton from San Francisco Bay to the Delta. *IEP Newsletter* 13(1):9-10.
- Rees JT, Gershwin LA. 2000. Non-indigenous hydromedusae in California's upper San Francisco Estuary: life cycles, distribution, and potential environmental impacts. *Scientia Marina* 64:73-86.
- Russell FS. 1953. The medusae of the British Isles I. Hydromedusae. Cambridge Univ Press. 530 p.
- Russell FS. 1970. The medusae of the British Isles II. Pelagic Scyphozoa. Cambridge Univ. Press. 284 p.
- Skogsberg T. 1948. Systematic study of the family Polyorchidae (Hydromedusae). *Proc Calif Acad Sci* 26:101-24.

Torrey HB. 1909. The leptomedusae of the San Diego region. Univ Calif Publ Zool 6:11-31.

Uchida T, Nagao Z. 1959. The life-history of a Japanese brackish-water hydroid, *Ostoumova horii*. J Fac Sci Hokkaido Univ (Ser. 6: Zool) 14:265-81.

Wrobel D, Mills CE. 1998. Pacific Coast pelagic invertebrates: a guide to the common gelatinous animals. Sea Challengers and Monterey Bay Aquarium. 108 p.

Notes

Bollens, Steve. San Francisco State University. Presentation in Monterey, Calif., December 1998.

Cohen, Andrew. San Francisco Estuary Institute. Specimens collected in a fish trap identified by J. Rees. 1997.

Foss, Steve. Marine/Fisheries Biologist. California Department of Fish and Game, Bay-Delta Division. Letter dated July 16, 1999.

Gartz, Russ. Marine/Fisheries Biologist. California Department of Fish and Game, Bay-Delta Division. Letter dated December 23, 1999.

APPENDIX A

Annotated List of Estuary Jellyfish

This list can be used in conjunction with the following field key (Appendix B). The list includes hydromedusae (class Hydrozoa), scyphomedusae (class Scyphozoa), and ctenophores (phylum Ctenophora) either collected by the authors or reported by the California Department of Fish and Game and/or U.S. Fish and Wildlife Service personnel as occurring in the estuary.

Phylum Cnidaria

Class Hydrozoa

This group contains the smaller jellyfish encountered in the field. All hydrozoan jellyfish that occur in the estuary have a persistent polyp stage. The class Hydrozoa is bedeviled with a "dual" classification system, one for benthic hydroids and a second for pelagic hydromedusae. This system is still in use primarily due to our incomplete knowledge of many hydrozoan life cycles. In extreme cases, hydroid colonies give rise to medusae known under different genera.

Order Anthomedusae

Amphinema sp. An undetermined introduced species of *Amphinema* has recently been found in Bodega Harbor growing on an introduced bryozoan. Conditions in San Francisco Bay are favorable for the growth of both the hydroid and its commensal bryozoan (Rees 2000).

Bougainvillia spp. There may be as many as three species of *Bougainvillia* hydroid polyps at Alameda Point, none of which have been identified or determined as native or introduced. At least one species releases free medusae.

Moerisia sp. An oligohaline to mesohaline form introduced into the estuary. The genus is thought to be a native of the Black and Caspian seas. This jellyfish is small (maximum bell height about 0.8 cm) and transparent. Distinguishing features are the cross-shaped translucent gonads of sexually mature adults. Adult medusae have 32 or fewer tentacles. The bell is usually higher than wide. The polyp of *Moerisia* was first described in error from the Petaluma River in 1993 (Mills and Sommer), as *Maeotias (marginata)*. This error was later addressed and corrected (Mills and Rees 2000). All *Moerisia* polyps from the estuary, either collected or reared in the laboratory, have been solitary. The polyp releases one medusa at a time. Polyps resemble *Hydra*, and have 10-12 highly extensile filiform tentacles scattered over the polyp body. Polyps are capable of rapid reproduction under suitable environmental conditions. Jellyfish of this species have to date been collected from Suisun Slough near the Suisun City Marina and the Napa River. Due to its small size and invisibility in turbid water, the medusa can be easily overlooked. Both the polyp and medusa are probably widespread throughout the upper estuary. The taxonomy of the entire family Moerisiidae is in need of revision, and in our present state of knowledge it is not possible to assign a species name to the form found in the estuary. *Moerisia* has also been reported from Chesapeake Bay by Calder (1971), as *M. lyonsi*. *M. lyonsi* reportedly forms multi-polyp colonies.

Polyorchis haplus (Skogsberg 1948). A very close relative of *P. penicillatus*. We collected this medusa at Alameda Point in 1999, the first record of this species in San Francisco Bay. It does not grow as large as *P. penicillatus* (to 2.5 cm bell height) and lacks the characteristic diverticulae of the radial canals found in *P. penicillatus*. As in *P. penicillatus*, the polyp is not known. For a review of both species of *Polyorchis*, see Skogsberg (1948).

Polyorchis penicillatus (Eschscholtz 1829). This native jellyfish, formerly more common and widespread throughout San Francisco Bay, is now found only sporadically and locally. The medusa is distinguished with a bell higher than wide hanging, sausage-shaped gonads, and red pigment and the base of the tentacles. The mature jellyfish is large, up to 5 cm bell height. Typically found in bays and harbors from Alaska to northern Baja California. Formerly common off the Berkeley pier and Berkeley Yacht Harbor, now seen only rarely. The medusa has appeared with regularity at the surface in the plankton at Alameda Point since 1995 from about October until the first heavy rains apparently drive the medusae to the bottom, generally in January. The medusa is somewhat mesohaline, and can tolerate brackish water down to about 23 ppt. We also have collected the medusa around the entrance to the Golden Gate. This beautiful jellyfish may have the distinction of being the first invertebrate described from California (Eschscholtz 1829). The polyp of this medusa is not known.

Sarsia spp. *Sarsia* medusae are characterized by having only four tentacles. Most *Sarsia* medusae are small, usually no more than 0.5 cm bell height. All *Sarsia* polyps have scattered capitate (club-shaped) tentacles and form colonies. *Sarsia* colonies occur in the fouling fauna in the central Bay and near the Golden Gate. Estuary species of *Sarsia* encountered can be either native or introduced. *Sarsia tubulosa* (M. Sars) is an introduced species found in Central Bay. Colonies of this species are present on pier spacers at Alameda Point. Mature medusae were reared from small medusae released from colonies, grown to adults in the laboratory, and identified by the authors. Mature medusae are small, about 0.2 to 0.3 cm bell height. This species has not been recorded from California previously and is probably an introduction. Other species present at Alameda Point include *Sarsia eximia* (Allman 1859) and *Sarsia vesicularis* n sp., which will be the subject of an upcoming paper (Rees forthcoming).

Scrippsia pacifica (Torrey 1909). A rarely encountered medusa, not known from San Francisco Bay until juveniles were collected at Alameda Point in 1996. Adults have subsequently also been collected in San Pablo and San Francisco bays. Mature adults are one of the most striking hydromedusae in the world, reaching bell heights of 10 cm. Identification of adults is unmistakable by virtue of their large size and tentacles, which ride up onto the exumbrella. The medusa has been collected at the Berkeley Yacht Harbor and caught in fish traps in San Pablo Bay (A. Cohen, personal communication). Like its relative *Polyorchis*, *S. pacifica*, is a native species and is apparently also a denizen of embayments along the California coast, although it has a more restricted distribution than the former, occurring from Fort Bragg to Bahia de Sebastian Vizcaino on the Pacific Coast of Baja California. It is less frequently seen and can be easily confused with *Polyorchis*, particularly in immature medusae. Nothing is known of its life cycle or its ecology. See Torrey (1909) for a discussion of the species.

Turritopsis nutricula (McCrary 1857). Mature medusae collected at Alameda Point. Medusa small, 0.2 to 0.3 cm bell height. Light's Manual states this may be a possible introduction. Polyp is not yet collected in the estuary.

Velella velella (Linnaeus 1758). An oceanic, neuston form (floating above the water), basically a floating upside-down polyp, commonly known as "by-the-wind sailor." Turns up in the Central Bay on occasion on the surface and washes up on Central Bay beaches. World-wide distribution occurs in tropical and temperate seas.

Order Leptomedusae

Blackfordia virginica (Mayer 1910). A mesohaline medusa introduced into the estuary. Probably

native to the Black and Caspian seas (Naumov 1960; Moore 1987). Originally described from the East Coast of the United States (Mayer 1910). Adult medusae are small (≤ 1.5 cm bell width) transparent, and have from 50-60 tentacles. The bell is wider than high. To date the jellyfish has been reported from the Napa and Petaluma rivers and the outer Delta near Chipps Island, although it is almost certainly more widespread. The polyp is very small (< 0.1 cm in height), colonial, and has been found growing on barnacles on floating docks in the Napa River. See Mills and Rees (2000) for a complete description.

Order *Limnomedusae*

Craspedacusta spp. (and *Limnognathia*) spp. These two genera are true freshwater jellyfish, and both are widely distributed. The systematics, ecology, and even morphology of these genera are confused and need clarification. *Craspedacusta* is apparently native to east Asia, whereas *Limnognathia* is native to the Great Lakes of the African rift. From 1997-1999, freshwater jellyfish were reported from several locales in California, including the upper Sacramento River near Redding, Folsom Lake, and two small man-made lakes in Mendocino and Sonoma counties. Since these jellyfish were not personally examined by the authors, we cannot confirm the identification of any of these medusae.

Maeotias marginata (formerly *inexpectata*) (Modeer 1791). An oligo- and mesohaline species introduced into the estuary. Purportedly native to the Black Sea. Originally described from the Netherlands in 1791 from collections made in 1765, and may have the distinction of being the first introduced invertebrate described in the literature. Adult medusae are distinct, being fairly large (up to 5 cm bell width), opaque (the bell can be tinged with brown or red), and with a distinct red or brown rim around the bell margin. Numerous tentacles in the adult (400 to 500). Confirmed collections of this jellyfish from the estuary have been from the Napa and Petaluma rivers, Suisun Slough and general Suisun Bay, and the outer Delta (Sacramento and San Joaquin rivers) in salinities down to 1 ppt. The polyp has not been described and is not known from the field. See Rees and Gershwin (2000) for a discussion of this species.

Proboscoidactyla spp. Medusae of this genus have been collected at Alameda Point. The hydroid is unique in possessing two tentacles and being obligate commensals on the rims of tubes of sabelid polychaetes. See Hand (1954) for a discussion of this genus in Central California. Mature medusa small, 0.2-0.4 cm bell height. The species found at Alameda has not been determined. All local species of *Proboscoidactyla* are native.

Class *Scyphozoa*

These are the larger jellyfish encountered in the field, and can attain large sizes, up to several meters in bell diameter, although estuary forms are smaller (usually up to 1/2-meter bell diameter). Like the hydromedusae, members of the group have a persistent benthic polyp stage, which buds tiny jellyfish in a process known as strobilization. Polyps of scyphozoans turn up in the fouling fauna in San Francisco and San Pablo bays, but none have been identified to species.

Aurelia aurita (Linnaeus 1758). Similar to *A. labiata* (below). Has a bell margin scalloped into eight instead of 16 lobes. Apparently an introduced species. So far localized around Foster City in the South Bay.

Aurelia labiata (Chamisso and Eysenhardt 1821). Has four lunate-shaped gonads in adults, hence the common name "moon jelly." This is apparently the native West Coast species, and is distin-

guished by a bell margin scalloped into 16 lobes. Bell is upwards of 50 cm in diameter. Seen at Alameda in late summer and fall. Moon jellies have been collected in San Francisco and San Pablo bays. See Greenberg and others (1996) for a discussion of the two species of *Aurelia* found in San Francisco Bay.

Chrysaora fuscescens (Brandt 1835). Bell up to 30 cm in bell diameter, with yellow-brown lines on the exumbrella. With 24 marginal tentacles. When present, found in the Central Bay and Golden Gate. Young medusae (10-15 cm in bell diameter) have been collected in spring near the Golden Gate. Native species.

Pelagia colorata (Russell 1964). Bell up to 70 cm in diameter, covered with bumps or warts. With eight long marginal tentacles. When present, found in the Central Bay and Golden Gate. Native species.

Phacellophora camtschatica (Brandt 1835). When viewed from above, the top of the bell has a central yellow mass surrounded by a whitish or pale yellow bell, hence the common name "fried egg jellyfish." With 16 clusters of tentacles. When present, found in the Central Bay and Golden Gate. Native species.

Cyanea capillata (Linnaeus 1758). Bell can be large, up to 100 cm in diameter. Color of the bell varies from deep red to purplish. When present, found in the Central Bay and Golden Gate. Native species.

Phylum Ctenophora

Ctenophores, in contrast to medusae, do not have a true bell. These animals propel themselves through the water with eight rows of comb cells, or "ctenae." Ctenophores are entirely pelagic and lack a benthic phase.

Pleurobrachia bachei (A. Agassiz 1860). Adults the size and shape of a clear marble, hence the common names, "cats' eyes" or "sea gooseberries." Common in the Central Bay around Alameda in the late summer and fall. Native species.

APPENDIX B

Field Key to the Larger and More Commonly Encountered "Jellyfish" in the San Francisco Estuary

1. Without true bell; animals size and shape of a 1 to 2 cm diameter clear marble;
does not pulse like a jellyfish, but "spins" as part of a feeding behavior.
Phylum Ctenophora.....*Pleurobrachia bachei*
With bell; animal pulsates to propel itself through the water column.....2
2. Bell higher than wide; smaller forms, both bell height and width 10 cm or less.....3
Bell wider than high, adult bell width not greater than 5 cm.....4
Bell wider than high, bell width from 10 cm to upwards of 70 cm in adults;
large, oceanic forms, found in Central Bay and Golden Gate area.
Class Scyphozoa (Scyphomedusae).....5
3. Small transparent medusae, adults to 0.5 (occasionally to 1.0) cm in bell
width; with a cross-shaped gonad; found in brackish water areas of
the upper estuary*Moerisia* sp.
Adults 8 to 10 cm in bell height; tentacles in adults rise about 1/5 of the
way up the external side of the bell; prominent red pigment patches at base
of tentacles.....*Scrippsia pacifica*
Adults to 4 cm in bell height; tentacles in adults rise only slightly above
bell rim; small red pigment patches at base of tentacles; lateral branches
on radial canals.....*Polyorchis penicillatus*
4. Bell reddish or brownish in hue with red-brown rim around bell margin;
bell width to 5 cm; curtain-like gonads in mature (> 2 cm) individuals;
found in brackish water areas of the upper estuary*Maeotias marginata*
Bell transparent; animals virtually invisible in turbid water;
bell diameter not greater than 2 cm; found in brackish water areas
of upper estuary*Blackfordia virginica*
5. Bell disc shaped; numerous small fringe-like marginal tentacles;
crescent or horseshoe-shaped gonads. *Aurelia*.....6
Bell either flattened or domed; marginal tentacles very long.....7
6. Manubrium small and inconspicuous; up to 50 cm bell diameter *Aurelia aurita*
Manubrium large and conspicuous, up to 1/3 in length of bell diameter
Bell up to 50 cm in diameter *Aurelia labiata*
7. Bell domed; marginal tentacles arranged singly8
Bell flattened; marginal tentacles arranged in groups.....9

8. Eight long marginal tentacles; bell of medusa whitish with 16 dark purple stripes; up to 70 cm bell diameter *Pelagia colorata*
Twenty-four marginal tentacles; bell with radial, pale yellow-brown streaks; up to 30 cm bell diameter..... *Chrysaora fuscescens*
9. Top of bell resembles a fried egg; translucent whitish bell with yellow center.....*Phacellophora camtschatica*
Color deep red to purplish; up to 1 meter in bell diameter *Cyanea capillata*

**ILLUSTRATIONS OF THE LARGER AND MORE
COMMONLY ENCOUNTERED "JELLYFISH"
IN THE SAN FRANCISCO ESTUARY**

John T. Rees
Bay-Delta Area Shore Institute
and
Department of Biological Sciences
California State University, Hayward

and

Christopher L. Kitting
Bay-Delta Area Shore Institute
and
Department of Biological Sciences
California State University, Hayward

All illustrations are by the authors unless otherwise noted.

Pleurobrachia bachei
(comb jelly ctenophore)

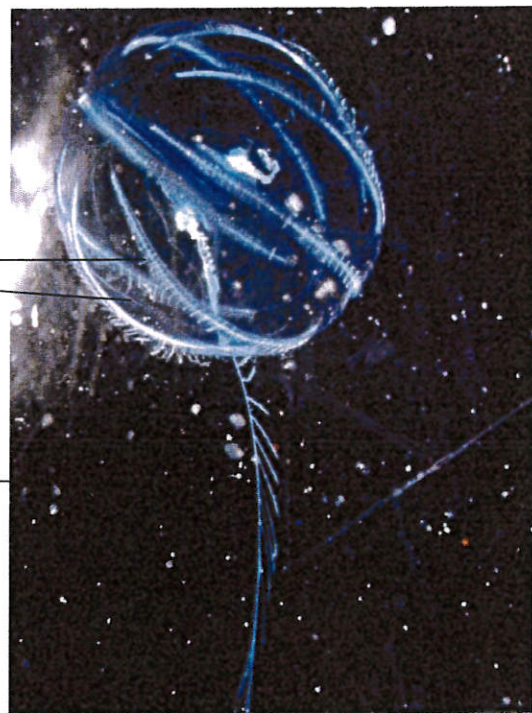
Color: Transparent

Size: Small, 1 to 2 cm, round; nicknamed “sea gooseberry”

Animal “spins” rather than pulsates

With eight comb rows, or “ctenae”

One pair of long “tentacles”



2X Life Size

Habitat: Central Bay, outer coast

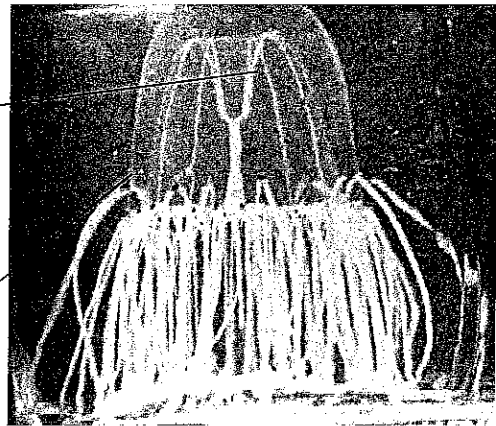
Scrippsia pacifica

Color: Bell transparent

Size: Large, up to 8 cm bell height

Large gelatinous peduncle with numerous gonads

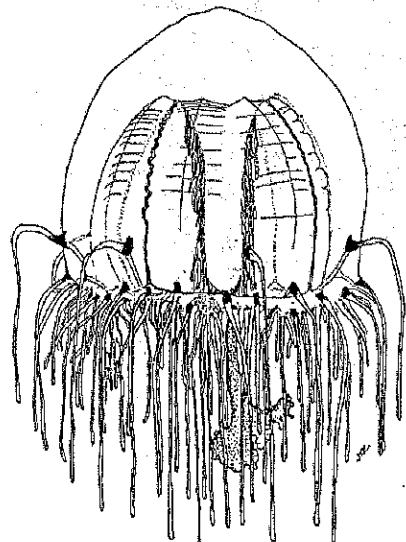
Bases of tentacles rise above the bell margin



Life Size

Reddish or purplish pigmented areas at base of tentacles

Areas found: San Francisco and San Pablo bays; tends to be near the bottom, and may be collected in trawls



1/2 Life Size

Polyorchis penicillatus

Color: Bell translucent to slightly milky

Size: Up to 5 cm bell height; bell higher than wide

Many diverticulae on radial canals

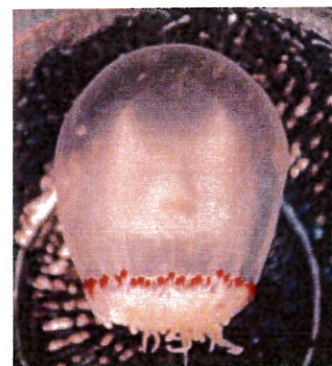
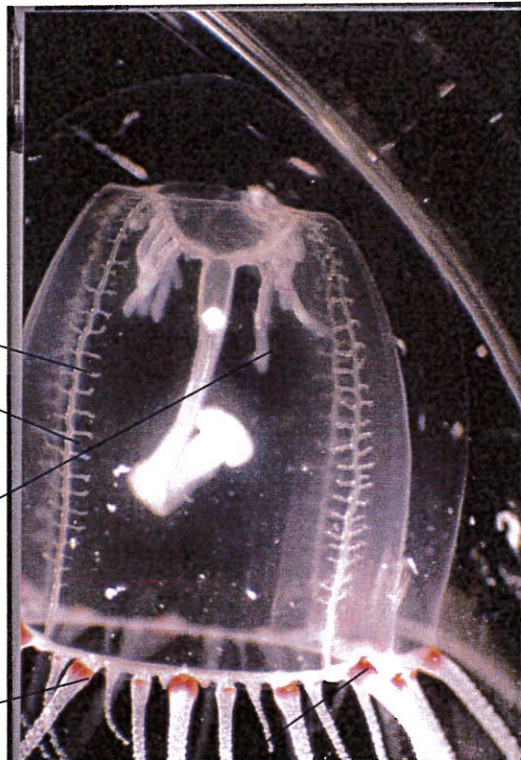
2X Life Size

Sausage-shaped hanging gonads

Red spot or pigment patch at base of each tentacle

Tentacle bases rise only slightly above bell margin

Areas found: San Francisco and San Pablo bays; near eelgrass beds, around docks and marinas



Life Size

Maeotias marginata

Color: Adults milky or dusky-colored with distinct reddish or brownish bell rim

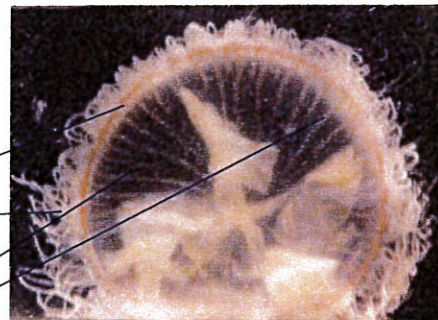
Size: Up to 5 cm bell diameter

Numerous tentacles (400 to 500) in adult medusae

Many secondary radial canals

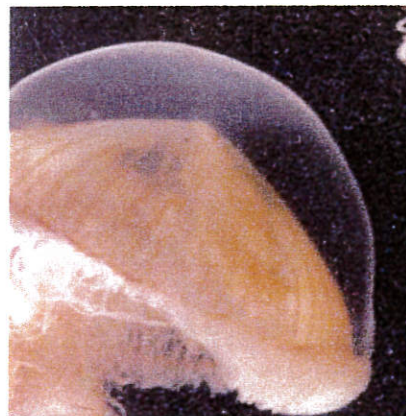
Four curtain-like hanging gonads

Oral View



Life Size

Side View



2X Life Size

Areas found: Upper estuary: Suisun Bay, Napa and Petaluma rivers

Blackfordia virginica

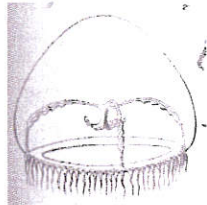
Color: Bell transparent; gonads and manubrium (lips) whitish

Size: Up to 1.5 cm bell width

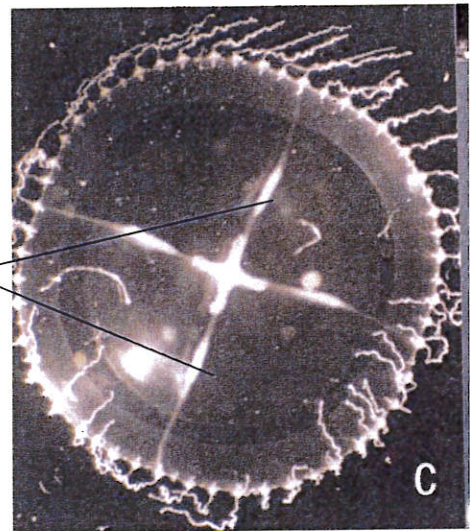
Bell wider than high

Gonads not continuous with manubrium

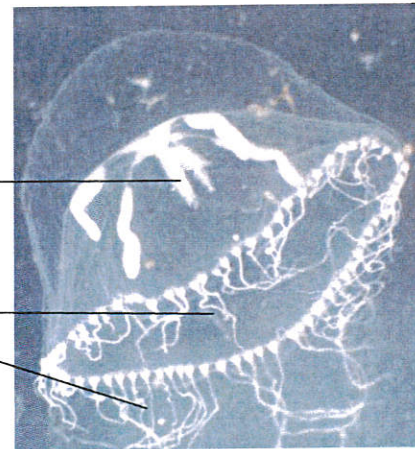
2X Life Size
From Mayer (1910)



Aboral View



Side View



Lips of manubrium

50 to 60 tentacles in adult medusae

Areas found: Upper estuary; Suisun Bay, Napa and Petaluma rivers

***Moerisia* sp.**

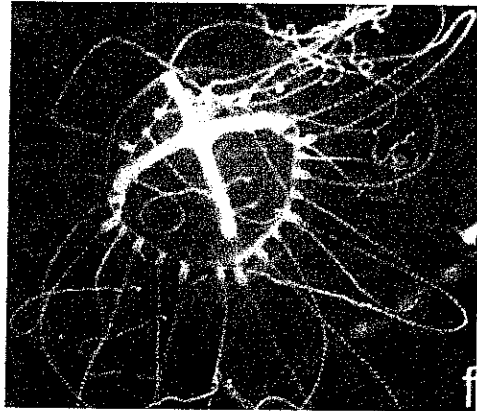
Color: Bell transparent

Size: Adults small, usually 0.5 cm or less in bell height

Gonads cross-shaped and continuous with manubrium

Up to 32 tentacles in adult medusae

Aboral View



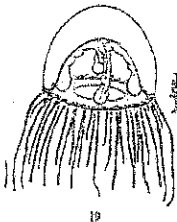
Side View



Bell higher than wide

Lips of manubrium compact

2x Life Size



From Uchida and Nagao (1959)

Habitat: Brackish-water areas in the upper estuary;
Napa River, Suisun Slough

Aurelia aurita
(moon jelly)

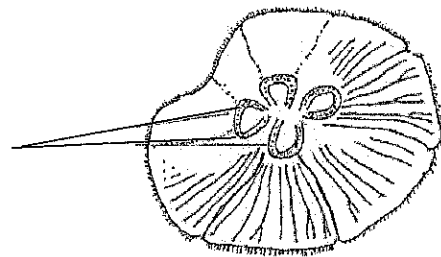
Color: Bell milky translucent

Size and shape: Bell much wider than high and dish-shaped; up to 50 cm bell width

Bell margin scalloped into eight distinct lobes

Aboral View

Four distinct horseshoe shaped gonads



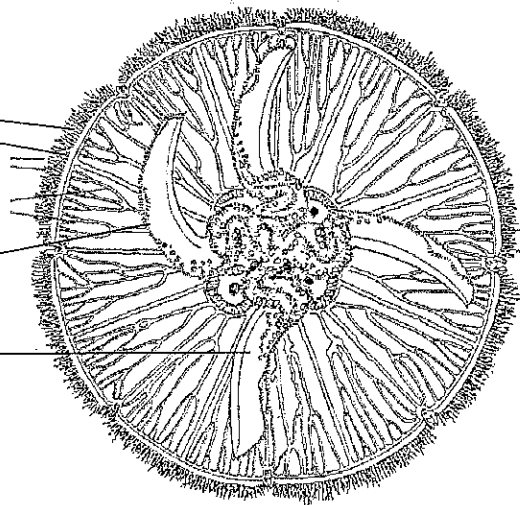
Oral View

Numerous tiny tentacles

Eight radial canals and numerous secondary canals

Oral arms

Short manubrium inside oral arms, less than 1/3 diameter of bell



Based on Russell 1970
1/3 Life Size

Areas found: San Francisco Bay and open coast

Aurelia labiata
(moon jelly)

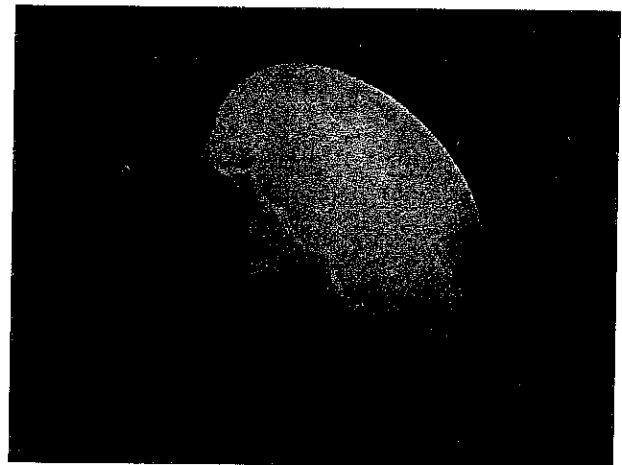
Color: Bell milky translucent

Size and shape: Bell much wider than high and dish-shaped; up to 40 cm bell width, or <70 cm bell width, offshore

Bell margin scalloped into sixteen lobes

Four distinct horseshoe shaped gonads

Numerous tiny tentacles



Eight radial canals and numerous secondary tentacles

Length of manubrium, when relaxed, is more than about 1/3 the bell diameter

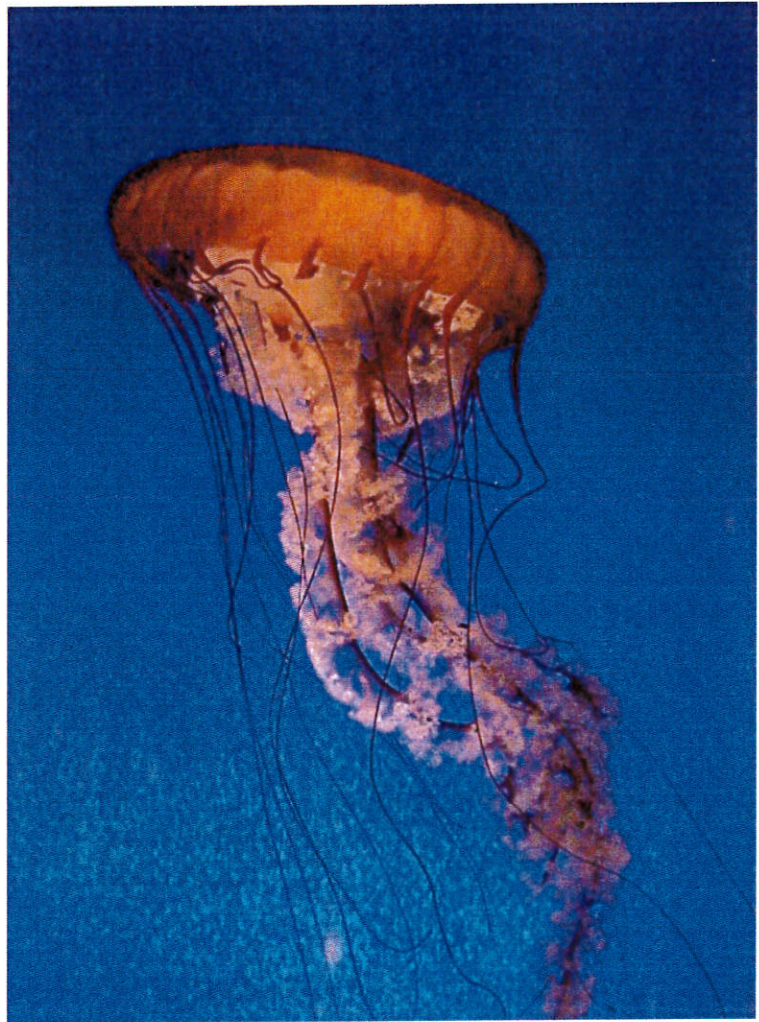
Areas found: San Francisco Bay and open coast

Chrysaora fuscescens

Color: Orange brown with sixteen radiating pale streaks on bell

Size: Up to 30 cm bell diameter

24-40 tentacles arising from bell margin



Habitat: Outer coast, San Francisco Bay. L. A. Gershwin recently confirmed that California's *Chrysaora* sp. is *C. fuscescens*, and *Chrysaora* systematics are under revision.

Pelagia colorata

Color: Bell color variable, usually yellow brown or silvery, with 16 purple radial stripes

Size and shape: Bell wider than high; 10 to 70 cm bell diameter

Eight long marginal tentacles spaced evenly around the bell margin

Manubrium and oral arms hang below bell 2 to 3 times bell radius



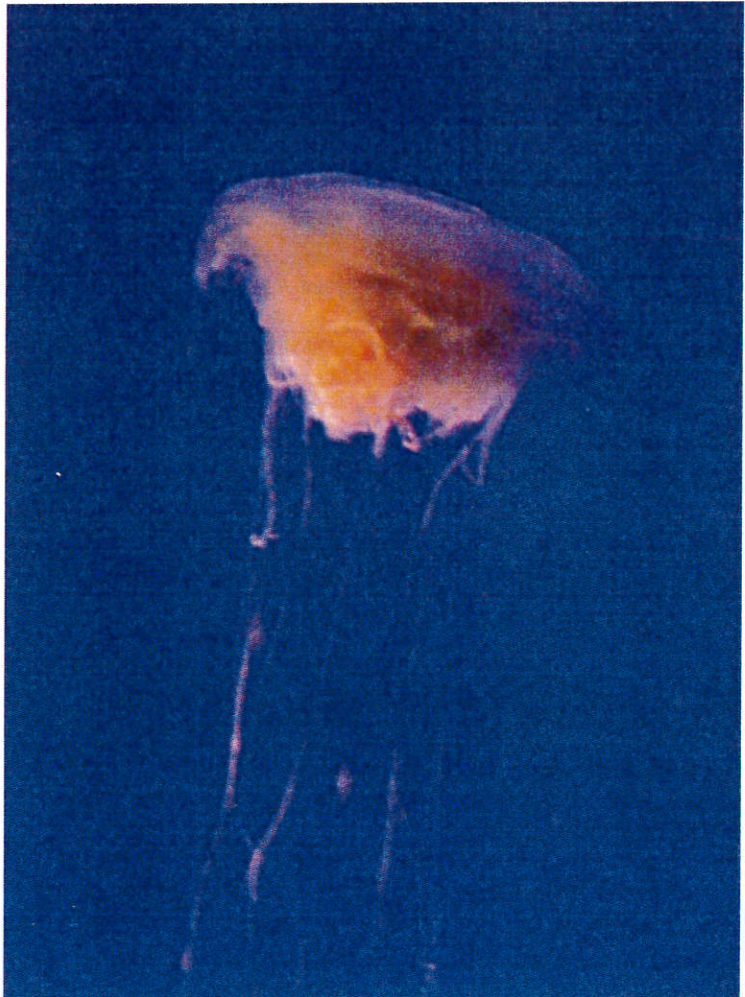
Areas: Oceanic genus, sometimes in San Francisco Bay

Cyanea capillata

Color: Medusa red to purplish

Size and shape: Large - up to 1 m bell width; bell disc-shaped

Bell divided into 8 thick lobes

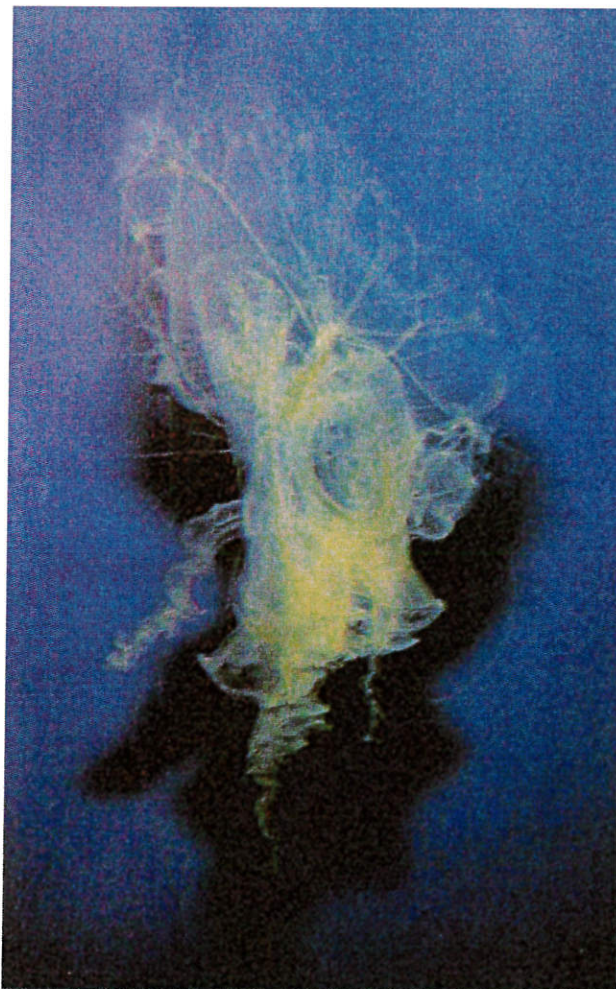


Areas found: Oceanic form; rare in Northern California

Phacellophora camtschatica
(Fried-egg jellyfish)

Color: Top of bell resembles a fried egg, with a yellow center and whitish or pale yellow outer portion

Size: Up to 60 cm bell width



Areas found: Outer coast and San Francisco Bay

